Comparison of the effects of artificial and natural barriers on large African carnivores: Implications for interspecific relationships and connectivity

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Abstract: Physical barriers contribute to habitat fragmentation, influence species distribution and ranging behaviour, and impact long-term population viability. Barrier permeability varies among species and can potentially impact the competitive balance within animal communities by differentially affecting co-occurring species. The influence of barriers on the spatial distribution of species within whole communities has nonetheless received little attention. During a 4-year period, we studied the influence of a fence and rivers, two landscape features that potentially act as barriers on space use and ranging behaviour of lions Panthera leo, spotted hyenas Crocuta crocuta, African wild dogs Lycaon pictus and cheetahs Acinonyx jubatus in Northern Botswana. We compared the tendencies of these species to cross the barriers using data generated from GPS-radio collars fitted to a total of 35 individuals. Barrier permeability was inferred by calculating the number of times animals crossed a barrier vs. the number of times they did not cross. Finally, based on our results, we produced a map of connectivity for the broader landscape system. Permeability varied significantly between fence and rivers and among species. The fence represented an obstacle for lions (permeability $= 7 \cdot 2\%$), while it was considerably more permeable for hyenas ($35 \cdot 6\%$) and wild dogs and cheetahs (50%). In contrast, the rivers and associated floodplains were relatively permeable to lions ($14 \cdot 4\%$) while they represented a nearly impassable obstacle for the other species (<2%). The aversion of lions to cross the fence resulted in a relatively lion-free habitat patch on one side of the fence, which might provide a potential refuge for other species. For instance, the competitively inferior wild dogs used this refuge significantly more intensively than the side of the fence with a high presence of lions. We showed that the influence of a barrier on the distribution of animals could potentially result in a broad-scale modification of community structure and ecology within a guild of co-occurring species. As habitat fragmentation increases, understanding the impact of barriers on species distributions is thus essential for the implementation of landscape-scale management strategies, the development and maintenance of corridors and the enhancement of connectivity.

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Comparison of the effects of artificial and natural barriers on large African carnivores: Implications for inter-specific relationships and connectivity

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Running title: Influence of barriers on large carnivores

SUMMARY

1. Physical barriers contribute to habitat fragmentation, influence species distribution and ranging behaviour, and impact long-term population viability. Barrier permeability varies among species and can potentially impact the competitive balance within animal communities by differentially affecting co-occurring species. The influence of barriers on the spatial distribution of species within whole communities has nonetheless received little attention.

2. During a 4 year period, we studied the influence of a fence and rivers, two landscape features that potentially act as barriers on space use and ranging behaviour of lions *Panthera leo*, spotted hyenas *Crocuta crocuta*, African wild dogs *Lycaon pictus* and cheetahs *Acinonyx jubatus* in Northern Botswana. We compared the tendencies of these species to cross the barriers using data generated from GPS-radio collars fitted to a total of 35 individuals. Barrier permeability was inferred by calculating the number of times animals crossed a barrier vs. the number of times they did not cross. Finally, based on our results, we produced a map of connectivity for the broader landscape system.

3. Permeability varied significantly between fence and rivers and among species. The fence represented an obstacle for lions (permeability = 7.2%), while it was considerably more permeable for hyenas (35.6%) and wild dogs and cheetahs (≥ 50%). In contrast, the rivers and associated floodplains were relatively permeable to lions (14.4%) while they represented a nearly impassable obstacle for the other species (< 2%).

4. The aversion of lions to cross the fence resulted in a relatively lion-free habitat patch on one side of the fence, which might provide a potential refuge for other species. For instance, the competitively inferior wild dogs used this refuge significantly more intensively than the side of the fence with a high presence of lions.

5. We showed that the influence of a barrier on the distribution of animals could potentially result in a broad-scale modification of community structure and ecology within a guild of co-occurring species. As habitat fragmentation increases, understanding the impact of barriers on species distributions is thus essential for the implementation of landscape-scale management strategies, the development and maintenance of corridors and the enhancement of connectivity.

Keywords: animal behaviour; coexistence; large carnivore guild; movement pattern; spatial distribution; spatial refuge; sympatric species

INTRODUCTION

Large-scale landscape features such as natural and artificial barriers contribute to habitat fragmentation and limit connectivity and can thus impact animal communities and threaten the long-term viability of species (McDonald & St. Clair 2004; Cozzi, Müller & Krauss 2008; Fahrig & Rytwinski 2009; Morales et al. 2010). Barriers have for instance been shown to alter ranging behaviour, dispersal, gene flow and distribution of a broad range of species (e.g. Shepard et al. 2008; Fahrig & Rytwinski 2009 and references therein, Tracey et al. in press). When species co-occur in a landscape system, differential effects of barriers may change the spatial distribution and overlap of species and thus community structure (Didham et al. 1996).

To date, however, the majority of the studies investigating the impact of barriers on free-ranging animals have focused on a single species (e.g. Trombulak & Frissell 2000 and examples therein; Dodd et al. 2007; Vanak, Thaker & Slotow 2010) rather than on entire communities or groups of species and their interactions. For example, Blanco et al. (2005) showed that a river constrained the range expansion of wolves *Canis lupus* in Spain, yet they did not examine the consequences of the changed spatial distribution of wolves on other competing predator species. Only a few studies have described the extent to which barriers might influence the spatial distribution of species within guilds or whole animal communities

(St. Clair 2003, McDonald & St. Clair 2004). If barriers affect species differentially, we would expect barriers to influence the spatial distribution and interactions among co-occurring species (Frantz et al. 2012). For example, the exclusion of a species incapable of crossing a barrier may release other species from competition and predation. Medium-sized predators are, for instance, believed to benefit from the removal of larger predators in mammalian carnivore guilds (Crooks & Soule 1999; Berger, Gese & Berger 2008).

The permeability of a barrier to animal movements mainly depends on the animal's perception, its needs and motivation to cross, and ultimately on the physical characteristics of both animals and barriers (Wiens, Crawford & Gosz 1985; McDonald & St. Clair 2004; Lagendijk et al. 2011; Frantz et al. 2012). Therefore, barriers will often limit connectivity among habitat patches and may intensify or reduce interactions among co-occurring species restricted within progressively smaller and more isolated habitat patches. For integrative species conservation management, barriers represent a particular concern and challenge because their effects on animal populations and community structure are difficult to predict (Bélisle & St. Clair 2001; Lagendijk et al. 2011; Slotow 2012). Thus, understanding the impacts of artificial and natural barriers on the ranging behaviour of animal species is essential to ensure connectivity among populations and for the successful implementation of conservation strategies for endangered species (e.g. Kaczensky et al. 2011; Zeller, McGarigal & Whiteley 2012; Tracey et al. in press).

In this paper we compared the influence of fences and rivers, two potential barriers, on large carnivores in the Okavango Delta in Botswana as a case study. In this region, the negative effects of fences have already been documented for wild ungulate species (Mbaiwa & Mbaiwa 2006; Bartlam-Brooks, Bonyongo & Harris 2011) but nothing is known about the effects of fences on space use and ranging patterns of large carnivores. The Okavango Delta is part of the five nations Kavango-Zambezi Rivers ecosystem (KAZA) transfrontier project and understanding the impact of barriers on species distributions is essential for the implementation of management strategies for an international project that aims at creating a protected area for wildlife across Africa.

In particular, we investigated the effects of one fence and three rivers on four co-occurring large carnivore species, the lion (*Panthera leo* Linnaeus), the spotted hyena (*Crocuta crocuta* Erxleben), the African wild dog (*Lycaon pictus* Temminck) and the cheetah (*Acinonyx jubatus* Schreber). Data were generated from GPS-radio collars fitted on a total of 35 individuals. We analysed, for each species, its use of space on both sides of the barriers, assessed barrier permeability and explored the spatio-temporal characteristics of crossing locations. We further investigated whether low barrier permeability resulted in reduced presence of competitively superior predator species in particular habitat patches that might be used more intensively by competitively inferior species. Finally, we used our results to develop a map of habitat connectivity for the broader landscape system.

MATERIAL AND METHODS

Study area

This study was carried out between 2007 and 2011 in the Okavango Delta, a wildlife-managed landscape system of roughly 20,000 km^2 in Northern Botswana. As explained below, the study area (centred at: S 19.523°; E 23.635°) included a 60 km section of a government constructed and maintained veterinary fence and three branches of the Okavango River (Fig. 1A).

The Southern Buffalo Fence

The Southern Buffalo Fence (hereafter referred to as the ‘fence’) is a 225 km veterinary fence that surrounds the perennial waters of the Okavango Delta. It was erected in 1983 with the main purpose of separating Cape buffalos (*Syncerus caffer* Sparrman) from cattle to hinder the transmission of foot-and-mouth disease. The fence is not electrified, is 1.6 m high and is composed of eight parallel smooth wires spaced at 20 cm intervals.

The northern side of the fence (hereafter referred to as the ‘wildlife side’) includes Moremi Game Reserve and the surrounding Wildlife Management Areas (Fig. 1A). In this area, photographic tourism and trophy hunting are the only permitted human activities. All major prey species of lion, spotted hyena, African wild dog and cheetah, such as Cape buffalo, zebra (*Equus burchelli)*, kudu (*Tragelaphus strepsiceros)*, impala (*Aepyceros melampus)*, warthog (*Phacochoerus aethiopicus)* and steenbok (*Raphicerus campestris)* (e.g. Hayward & Kerley 2008), are common on the wildlife side of the fence (G. Cozzi, unpubl. data).

The southern side of the fence (hereafter referred to as the ‘livestock side’) is dominated by cattle farms practicing subsistence pastoralism. A total of 36 farms are situated within 10 km of the fence; the mean number of livestock animals per farm is 47 (min. 5; max. 164) (data from Sebogiso et al., in prep.). Natural prey species have been recorded on the livestock side but their occurrence is rare (G. Cozzi, pers. obs.). Predator species may compensate for the limited abundance of natural prey on the livestock side by preying upon livestock. Among the four species investigated here, spotted hyenas were reported causing the majority of the losses, while the other species predated livestock less frequently (Gusset et al. 2009, O. Sebogiso pers. comm.). Because tolerance of predators depends on the extent of predation, and because the Botswana government does not compensate livestock losses to hyenas, farmers are particularly intolerant towards this species (O. Sebogiso pers. comm.).

Rivers

Three branches of the Okavango River cross the study area: the Gomoti, the Santantadibe and the Khwai Rivers (Fig. 1A). In the study area, the amount of water and the through-flow in the three rivers (they variably terminate in the Kalahari sands of northern Botswana) typically peak in July and subside rapidly reaching the lowest level early in the year. Overall, water levels in the rivers consistently increased between 2007 and 2011 due to exceptional rains. The sections of the three rivers within the study area never dried out during the study period, while the rivers occasionally dried at their distal terminus.

Field work and data collection

We systematically recorded location data of individual lions, spotted hyenas, African wild dogs and cheetahs using programmed GPS radio-collars (Vectronic Aerospace GmbH, Germany). As required by law, target animals were immobilized for collaring purposes by a qualified wildlife veterinarian using approved techniques and drug combinations (Osofsky, McNutt & Hirsch1996, Kock, Meltzer & Burroughs 2006). All captures took place north of the fence and east of the Gomoti River (with the exception of a dog resident in a pack on the western side). The data presented here are from fourteen lions in six prides, ten spotted hyenas in six clans, six African wild dogs in four packs and five individual cheetahs (Fig. S1–S4 in Supporting Information).

The collars were scheduled to record several GPS locations per day. For lions and hyenas, one location was recorded every two hours between 18:00 and 06:00 and one location was recorded at noon, giving a total of eight GPS locations per day. For wild dogs, GPS locations were recorded at 06:00, 12:00 and 18:00, and for cheetahs at 06:00, 12:00, 18:00 and 24:00. On average, collars successfully recorded 84.8 ± 3.20% (mean ± s.e.m) of the scheduled locations. In a test, 14 randomly selected collars were placed at known GPS locations under thick canopy cover and the distance between each GPS location collected by the collars and their actual location was measured in ArcGIS 9.2 (ESRI, United States). The GPS locations (n = 246) collected by the test collars were used to predict their accuracy, which was 11.62 m ± 4.05 m (mean ± s.e.m), and was assumed to be representative for the accuracy of all collars deployed in the field.

Space use

To investigate space use in the vicinity of a barrier we analysed for each individual and species the distribution of all GPS locations within 5 km on either side of each barrier. This measure was chosen to be larger than the average distance between two consecutive GPS locations moved by wild dogs, the most mobile of the four species, which was 3.53 ± 0.15 km (mean ± s.e.m.), and thus considered adequate to capture important ecological processes. We limited our analysis to the locations in the vicinity of the barriers because we had insufficient information about additional covariables (i.e. in addition to distance from the barrier), which might affect the animals' distributions further away from the barriers. We expected that if a barrier did not influence the use of space we would not observe a significant difference in the distribution of GPS locations on either side of the barrier; instead we would only observe a gradual decrease in the number of GPS locations the further away an animal is from the core of its territory. In contrast, an abrupt change in the number of GPS locations between the two sides of a barrier would suggest an effect of the barrier on an animals' use of space. Because the spatio-temporal autocorrelation structure of the data gives information about an animal's perception of the surrounding landscape, we did not subsample from the location time series of individual animals and instead retained all data within 5 km on either side of the barriers (Legendre 1993; Willems & Hill 2009).

Within this 5 km range, locations were binned to investigate the relationship between the number of locations and the distance to the barrier. We defined 100 m wide bins and we then calculated, for each species and barrier type, the average number of GPS locations within each bin (because not all individuals were recorded within each bin, averages allowed avoiding zero-inflation-related issues). Bin width was chosen to avoid excessive binning, yet without smoothing actual displacements, (for example, resting animals may move a few tens of meters to keep in the shade; G. Cozzi pers. obs.). The average number of GPS locations in each bin was used as the response variable in a polynomial model with distance from the barrier and its square (distance^2 = area), barrier side (N and S for the fence and W and E for the rivers) and interaction between distance and barrier side as predictor variables. The response variable was log-transformed to meet the assumption of normality of residuals. Clusters of GPS locations known to correspond to den sites or large carcasses (i.e. elephants *Loxodonta africana* Blumenbach and giraffes *Giraffa camelopardalis* Linnaeus) were treated as outliers and, unless specified, removed from the models. For all statistical analyses, model simplification startied from a full model and followed a backward selection procedure based on the Akaike Information Criterion (Zuur et al. 2009).

Crossing likelihood and movement metrics

We investigated the likelihood of crossing a barrier by calculating the number of times animals crossed a barrier vs. the number of times they had the potential to cross a barrier but did not. For each individual, we created a continuous movement path by connecting consecutive GPS locations using Hawth’s Tools for ArcGIS 9.2 (Beyer 2004). The segment between two consecutive GPS locations is hereafter referred to as a ‘step’. Steps that had at least a portion of their length within a distance from the barrier equal to half the average step length (specific to each individual) were considered as potential crossing events. To each one of these potential crossing events, we assigned a value of '1' if the animal crossed a barrier and a value of '0' if the animal did not. Because the criterion of half the average step length is somewhat arbitrary, we repeated the analysis considering all steps within a distance equal to the full average step length. The qualitative outcome remained unchanged and we therefore present only the results derived from data selected using the criterion of half the average step length. We analysed crossing likelihood using a generalized linear mixed-effects model (GLMM) with binomial distribution and accounted for over-dispersion of the data. Steps (crossing vs. non crossing) were entered as binary response variable; barrier type (i.e. fence or river) animal species and year (as a proxy for the increasing water level) were entered as fixed effects; animal identity was entered as random effect.

To further investigate the influence of a barrier on animal movement patterns, we investigated net displacement between four consecutive steps (i.e. the distance between the beginning of $step_i$ and the end of $step_{i+4}$) in the vicinity of the barriers (i.e. within a distance of half the average step length) and at random locations away from the barriers. Furthermore, we analysed the directionality of the steps in the vicinity of the fence (the same analysis was not done for the rivers due to their tortuosity). To each step we assigned a bearing between 0° and 90°. A step of 0° thus represented a movement perpendicular to the barrier and a step of 90° a step parallel to the barrier (no distinction was made if an individual was moving eastward: 90°, or westward: 270°). The necessary corrections were made for the diagonal (western) and vertical (eastern) section of the fence (see Fig. 1A). Steps shorter than 50 m were not considered because they were more likely to represent a stationary than a movement event. The bearing of each step was entered in a mixed-effects model with species as fixed explanatory term and individual as random term. Because angles were bound between 0° and 90°, we used the following transformation to meet assumptions of normality: $\mathrm{y} = \sin^{-1}\sqrt{\mathrm{A}}$; where: $A = angle/(\frac{\pi}{2})$. Species showing a predicted bearing smaller than 45° were consequently considered to mainly move to and from or across the fence, species showing an angle larger than 45° were considered as mainly moving along the fence.

RESULTS

Not all individuals had contact with both barriers (defined as recording at least one GPS location within 100 m from a barrier). Nine lions had contact with the fence but only four were recorded on both sides. The same applied to seven of nine spotted hyenas, all wild dogs and one of two cheetahs. Thirteen lions ad contact with the river and nine of them were recorded on both sides. Similarly, one of six spotted hyenas, one of four wild dogs and three of five cheetahs were recorded on both sides. Individuals reached the other side of a barrier in different ways. Our GPS records indicated, for example, that one hyena, one wild dog and one cheetah travelled around the drying terminus of the Gomoti River on several occasions rather than crossing it (see below and Fig. 1B), while lions crossed the river and inundated floodplains directly.

Space use

We observed a significant decrease in the number of lion GPS locations from the wildlife side to the livestock side of the fence (distance by side interaction term: $F_{1,95} = 13.99$, $p < 0{,}001$) (Table S1 & Fig. 2A & 2C). In contrast, spotted hyenas, wild dogs and cheetahs were not negatively influenced by the fence, and instead showed a steady decrease in the number of GPS locations with increasing distance from the core area of their territory (i.e. moving from north to south) (Table S1 & Fig. 2A & 2C). Wild dogs even showed a marginally significant increase in the number of locations on the livestock side of the fence ($F_{1,96} = 2.81$, $p = 0.097$). This figure was highly significant ($F_{1,96} = 10.67$, $p = 0.002$) when we retained in the analysis locations around the den site (Table S1 & Fig. 2A).

For all four species, there was a significant difference in space use (i.e. number of GPS locations) between opposite sides of the rivers (polynomial distance by side interaction term: lions: $F_{2,94} = 24.76$, $p < 0.001$; spotted hyenas: $F_{2,94} = 20.01$, $p < 0.001$; wild dogs: $F_{2,94} = 15.80$, $p < 0.001$; cheetahs: $F_{2,94} = 32.84$, $p < 0.001$) (Table S1 & Fig. 2B &2C). For hyenas, cheetahs and wild dogs this difference represented an almost complete lack of locations on the western side of the river, while for lions this difference resulted from the evident decrease of locations in the immediate vicinity of the western side of the river (cf. Fig. 2B, lion panel).

Crossing likelihood and movement metrics

Our results showed a significant difference among species in the crossing likelihood (interaction term barrier by species: $F_{3,20} = 87.69$, $p < 0.001$). In general, the response of lions was the inverse of the other species (Fig. 3A). Lions had a fence-crossing likelihood equal to 3.6% meaning that they crossed the fence 3.6 times for every 100 'steps' they made in its vicinity. In contrast, spotted hyenas, cheetahs and wild dogs had fence-crossing likelihoods of 17.8%, 25.5% and 30.7%, respectively. In contrast, water bodies were almost impermeable to spotted hyenas, wild dogs and cheetahs while they were considerably more permeable for lions (Fig. 3A). The river-crossing likelihood for lions was 7.2%, and was one to two orders of magnitude higher than the permeability for cheetahs, wild dogs and spotted hyenas, which were, respectively, 0.8%, 0.6% and 0.1%. We could furthermore detect a significant negative trend in river-crossing likelihood across years ($F_{4,1693} = 11.2$, $p < 0.001$), with 2007, the driest year, being characterized by the highest crossing likelihood (Fig. 3B).

Because, under an assumption of random movement, half the number of steps in the vicinity of a barrier are expected to end in the animal crossing and the other half in the animal not crossing a 50% crossing likelihood is equal to a 100% barrier permeability. If we correct for this factor, fence permeability for the smaller wild dog and cheetah was higher than 50%, for the medium-sized spotted hyena was 35.6 % and for the larger lion was only 7.2%. River permeability was 14.4% for lions and less than 2% for the other three smaller species.

We found that species net displacement varied significantly depending on the animals' location, i.e. in the vicinity of the fence, in the vicinity of the rivers, or further away from any barrier ($F_{6,3908} = 6.68$, $p < 0.001$). In particular, within species, lion and cheetah displacement near the rivers was considerably shorter than at random locations away from any barrier. Hyena net displacement was, instead, considerably shorter in the vicinity of the fence. We did not detect any significant differences for wild dogs (Fig. 3C). Note that because of differences in the collection of GPS data (see Methods), direct comparison across species is only possible between lions and hyenas. The movements in the vicinity of the fence were also significantly different between the four species ($F_{1,3} = 12.44$, $p < 0.001$). In particular lions, which tended to move along the fence, differed considerably from hyenas and wild dogs both of which tended to move more perpendicularly to it (Fig. 3D). Cheetah movements could not be classified in this way because only two cheetahs had contact with the fence; one crossed while the other never did.

Characteristics of crossing locations

Given the relatively small number of fence crossing events for lions (n = 24), crossing points were visually investigated. On ten occasions (41.7%), lions crossed the fence in the immediate vicinity of the floodplains associated with the Gomoti and Santantadibe Rivers where the fence had been observed to be in very poor conditions (see Hydrology section in Supporting Information). All ten crossing events occurred during 2007 and 2008, between mid September and mid November, a period that coincided with a low water level; no crossing events along floodplains were recorded during 2009–2011. No distinct characteristics were found for the other 14 crossing points. Spotted hyenas (n = 732 crossings), wild dogs (n = 145 crossings) and cheetahs (n = 16 crossings) crossed at any point along the entire length of the fence. Similarly, lions crossed at any point along the course of the rivers. After we corrected for the number of locations within each month, crossing frequency peaked towards the end of a calendar year, the time when water levels were lowest. Crossing frequency for lions was highest during 2007 and lowest during 2011. The only hyena that crossed the river did so three times within 24 hours at what appears to be one single crossing point. The same hyena circumvented the Gomoti on three occasions between December 2007 and January 2008. Similarly, the only wild dog that was recorded on both sides of the Gomoti circumvented it three times and crossed it once in February 2009. Evidence suggests that the crossing location corresponded to the only location known to the authors for crossing by car along an exposed sand bank. One cheetah circumvented the Gomoti during August and September 2010 (high water level) but never crossed it, while two other cheetahs crossed the river on three occasions.

DISCUSSION

Investigating the distribution and ranging behaviour of animal species in relation to various types of artificial and natural barriers is fundamental to assessing their aptitude for traversing obstacles, understanding the spatial relationships between co-occurring species, and to managing connectivity between suitable habitat patches (Didham et al. 1996; McDonald & St. Clair 2004; Blanco, Cortés & Virgós 2005; Kaczensky et al. 2011; Zeller, McGarigal & Whiteley 2012). Our results based on simultaneous observations of four species of the African large predator guild in northern Botswana demonstrate that the permeability of a barrier can vary considerably among taxonomically related species. We showed that lions were strongly restricted by a not-electrified eight-strand smooth wire veterinary fence built to control the movements of ungulate species. The same fence had no obvious effect on the ranging behaviour of the smaller spotted hyenas, wild dogs and cheetahs. It should be noted, however, that the results of the influence of the fence on cheetahs are based on only two individuals (one which crossed and which did not). Nevertheless, a similar limited effect of cattle fences can be anticipated for Namibia, where the majority of cheetahs live and moves on farmlands subdivided by fences similar to the one in our study area. In contrast to the effects of fences, lions regularly crossed rivers and associated floodplains, while the same expanses of water constituted comparatively impermeable barriers to the three other species (see Hydrology section in Supporting Information for a further discussion). The physical characteristics of a barrier and species-specific behaviours (cf. Fig. 3C & 3D) thus appear to be important characteristics in determining the permeability of a barrier (Wiens, Crawford & Gosz 1985; Clevenger & Waltho 2000, Kerth & Melber 2009). Substantial structural differences between barrier types may further influence an animal's perception resulting in differential likelihood of crossing.

Our findings emphasise that because barrier permeability varies among the members of a community, barriers can influence the spatial distribution and relationship of otherwise co-occurring species by excluding some species but not others from particular habitat patches, thus affecting community structure. Exclusion of competitively dominant species may trigger a succession of downward cascade events that influence community assembly (Lagendijk et al. 2011, Slotow 2012). This shows the importance of a multi-species approach where functionally sympatric groups of animals are considered simultaneously. A possible explanation of the observed ranging behaviour of the competitively inferior species (i.e wild dogs and cheetahs) on the livestock side of the fence could suggests that these may benefit from competition and predation release due to a lower lion presence. Predation by lions is a major cause of natural mortality in adult and juvenile wild dogs, particularly during the denning period (Mills & Gorman 1997). This antagonistic relation might explain the increased presence of wild dogs on the livestock side of the fence during times of the year when they were denning (Fig. 2A). This hypothesis is in line with a study by van der Meer et al. (2011) who concluded that a higher risk and cost of kleptoparasitism inside Hwange National Park might have contributed to habitat choice of African wild dogs outside the park. The GPS data from our study showed that the wild dogs, which denned south of the fence (data not shown) daily returned to the wildlife side instead of hunting on the livestock side, thus weakening the alternative hypothesis that the presence of wild dogs south of the fence was due to an easily accessible prey base (small stock). These interspecific dynamics are also consistent with findings from Namibia where cheetahs are reported to thrive on farmland due to the low density of lions outside protected areas (Marker-Kraus 1996). No such pattern was detected for cheetahs in our study, possibly due to the small sample size.

Following the proposed competition exclusion hypothesis, the fence may in effect encourage species that seek spatial refuge from superior competitors to move closer to human activities where they eventually suffer direct persecution (Balme, Huner & Slotow 2010; van der Meer et al. 2011). This may finally function as an ecological trap where the high mortality rate outside protected areas can have negative consequences on protected populations (Balme, Hunter & Slotow 2010). This possible scenario should be carefully taken into consideration for the conservation of species such as the African wild dog and the cheetah that are listed as endangered and vulnerable, respectively, according to the International Union for Conservation of Nature (IUCN). We nonetheless acknowledge that other confounding variables, such as species-specific habitat suitability or small-scale prey distribution, may influence the observed patterns. We therefore encourage that these alternative hypotheses be explored in the future.

In contrast to our observations, lions have been reported to frequently cross (electrified) fences in several other parts of Africa. The main reason for this permeability has been attributed to a lack of maintenance and the poor conditions of the fences (Stander 1990, Funston 2001, Hemson 2003). The well-maintained nature of the Southern Buffalo Fence may thus have been a major cause for the pattern observed in this study. Our conclusion is supported by the fact that in 41.7% of the observed crossing events, lions crossed near sections of the fence destroyed by water (see Hydrology section in Supporting Information). Because the utility of a fence is related to the costs of building and maintenance it and its effectiveness in controlling animal movements (e.g. Vercauteren, Lavelle & Hygnstrom 2006; Slotow 2012), our findings have economic implications. More research on this topic would be necessary for a full cost-benefit analysis. A low but well-maintained fence might thus be more effective in controlling lion movements than an electrified but damaged fence. The low presence of lions on the livestock side of the fence in our study was additionally supported by an extensive questionnaire survey (O. Sebogiso pers. comm.) and by spoor surveys carried out during this study (data not shown). Also consistent with these observations, farmers in the area adjacent to our study populations reported that livestock losses from lions were lower than losses from spotted hyenas (Gusset et al. 2009). Despite being erected for other purposes, the fence thus proved effective in reducing human-wildlife conflict with lions, which could be further improved with more consistent maintenance. We encourage further investigation to explore the potential of cattle fences to protect livestock or villages. Alternatively, a lack of motivation to cross, possibly due to the high abundance of prey species on the wildlife side, may also have influenced the lions' distribution across the fence.

The negative relationship between crossing likelihood and water levels across years (Fig. 3B) shows how the changing hydrology of the Okavango influences movements across rivers. The Okavango is an extremely dynamic system historically characterized by conspicuous, natural hydrological fluctuations. Our work, however, anticipates how changes in water levels, which in the coming years are likely to increase under the influence of climate change (e.g. Aldous et al. 2011), could change the dynamics of other inland systems that are historically more stable. This case study represents an additional example of the need to incorporate the effects of changing hydrology, and more in general climate change, on the management policies of protected areas (e.g. Hannah 2010; Groves et al. 2012).

The obstacles represented by the fence and the rivers have major consequences for habitat connectivity in the Okavango Delta. The rivers that run north–south represented a barrier to the west–east movements of spotted hyenas, wild dogs and cheetahs and to a lesser extent of lions. During wet years (e.g. this study), when all rivers flow past the fence, connectivity between habitat patches may be almost entirely granted by individuals travelling around the drying terminus of the rivers through the hostile farming area south of the fence (Fig. 1). During periods of droughts, however, when water levels are lower and river permeability increases (Fig. 3B), connectivity may be granted north of the fence by movements across the rivers or across dry sections of the rivers. It is beyond the scope of this paper to exactly quantify connectivity between habitat patches; however, it seems that the southern region of the Delta, where human activities concentrate, is essential in maintaining habitat connectivity within and across the broad landscape system. Similarly, it has been shown that the effects of conservation schemes outside protected areas can positively influence conservation within such areas (Balme et al. 2009). We therefore encourage educational schemes, which enhance tolerance towards carnivores and protection of predator species through implementation of a wildlife–friendly law. This should be included in the larger concept of the KAZA transfrontier project for the Okavango ecosystem.

This study demonstrated that the permeability of different types of barriers can vary widely among species. Variable permeability can directly and indirectly (e.g. through reduced competition) affect the distribution of animal species and lead to shifts in community structure different abundances in habitat patches. The previously documented effects of barriers on the distribution, dispersal behaviour, social structure and gene flow of species will thus also be combined with changes in species composition. These results emphasize the need for multi-species approaches in landscape-scale studies and planning.

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REFERENCES

Aldous, A., Fitzsimons, J., Richter, B. & Bach L. (2011) Droughts, floods and freshwater ecosystems: evaluating climate change impacts and developing adaptation strategies. *Marine & Freshwater Research*, 62, 223-231

Balme, G.A., Hunter, L.T.B. & Slotow, R.O.B. (2010) Edge effects and the impact of non−protected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa. *Animal Conservation*, 13, 315-323

Balme, G.A., Slotow, R.O.B. & Hunter, L.T.B. (2009) Impact of conservation interventions on the dynamics and persistence of a persecuted leopard (*Panthera pardus*) population. *Biological Conservation,* **142,** 681-2690

Bartlam-Brooks, H.L.A., Bonyongo, M.C. & Harris, S. (2011) Will reconnecting ecosystems allow long-distance mammal migrations to resume? A case study of a zebra Equus burchelli migration in Botswana. *Oryx,* **45**, 210-216

Bélisle, M. & St. Clair, C.C. (2001) Cumulative effects of barriers on the movements of forest birds. *Conservation Ecology,* **5, 9** URL:http://www.consecol.org/vol5/iss2/art9/

Berger, K.M., Gese, E.M. & Berger, J. (2008) Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. *Ecology***, 89**, 818-828

Beyer, H.L. (2004) Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Blanco, J.C., Cortés, Y. & Virgós, E. (2005) Wolf response to two kinds of barriers in an agricultural habitat in Spain. Canadian Journal of Zoology, **83**, 312-323

Clevenger, A.P. & Waltho, N. (2000) Factors Influencing the Effectiveness of Wildlife Underpasses in Banff National Park, Alberta, Canada. *Conservation Biology,* **14**, 47-56

Cozzi, G., Müller, C. & Krauss, J. (2008) How do local habitat management and landscape structure at different spatial scales affect fritillary butterfly distribution on fragmented wetlands? *Landscape Ecology,* **23**, 269-283

Crooks, K.R. & Soule, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563-566

Didham, R.K., Ghazoul, J. Stork,N.E. & Davis A.J. (1996) Insects in fragmented forests: a functional approach. *Trends in Ecology & Evolution,* **11**, 255-260

Dodd, N.L., Gagnon, J.W, Boe, S. & Schweinsburg, R.E. (2007) Assessment of elk highway permeability by using global positioning system telemetry. *The Journal of Wildlife Management*, **71**, 1107-1117

Fahrig, L. & Rytwinski, T. (2009) Effects of Roads on Animal Abundance: an Empirical Review and Synthesis. Ecology and Society, **14**, p. 21, http://www.ecologyandsociety.org/vol14/iss1/art21/

Funston, P.J. (2001) *Kalahari Transfrontier Lion Project: Final Report*. South African National Parks and Botswana Department of Wildlife and National Parks.

Frantz, A.C., Bertouille, S., Eloy, M.C., Licoppe, A. Chaumont, F. & Flamand, M.C. (2012) Comparative landscape genetic analyses show a Belgian motorway to be a gene flow barrier for red deer (*Cervus elaphus*), but not wild boars (*Sus scrofa*). *Molecular Ecology*, 21, 3445-3457

Groves, C.R, Game, E.T., Anderson, M.G., Cross, M., Enquist, Ferdaña, Z., Girvetz, E., Gondor, A., Hall, K.R., Higgins, J., Marshall, R., Popper, K., Schill, S. & Shafer, S.L. (2012) Incorporating climate change into systematic conservation planning. *Biodiveristy and Conservation*, 21, 1651-1671

Gusset, M., Swarner, M.J., Mponwane, L., Keletile, K. & McNutt, J.W. (2009) Human–wildlife conflict in northern Botswana: livestock predation by Endangered African wild dog *Lycaon pictus* and other carnivores. *Oryx*, **43**, 67 – 72

Hanna, L. (2010) A global conservation system for climatic-change adaptation. *Conservation Biology*, 24, 70-77

Hayward, M.W. & Kerley, G.I.H. (2008) Prey preferences and dietary overlap amongst Africa's large predators. *South African Journal of Wildife Research*, 38, 93-108.

Hemson, G. 2003. *The ecology and conservation of Lions: human-wildlife conflict in semi-arid Botswana*. PhD Thesis, University of Oxford, Oxford

Kaczensky, P., Kuehn, R., Lhagvasuren, B., Pietsch, S. Yang, W. & Walzer, C. (2011) Connectivity of the Asiatic wild ass population in the Mongolian Gobi. *Biological Conservation*, 144, 920-929

Kerth, G. & M. Melber, M. (2009) Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biological Conservation,* **142**, 270-279

Kock, M., Meltzer, D. & Burroughs R. (2006) *Chemical and Physical Restraint of Wild Animals: A Training and Field Manual for African Species*. International Wildlife Veterinary Services, Johannesburg, SA

Lagendijk, D.D.G., Mackey, R.L., Page, B.R. & Slotow R.O.B. (2011) The effects of Herbivory by a mega- and mesoherbivore on tree recruitment in sand forest, South Africa. PLoS ONE, **6**: e17983. doi:10.1371/journal.pone.0017983

Legendre, P. (1993) Spatial autocorrelation: Trouble or new paradigm? *Ecology***, 74**, 1659-1673

Marker-Kraus, L. 1996. *Cheetah survival on Namibian farmlands*. Cheetah Conservation Fund, Windhoek, Namibia

Mbaiwa, J.E. & Mbaiwa, O.I. (2006) The effects of veterinary fences on wildlife populations in Okavango Delta, Botswana. *International Journal of Wilderness***, 12**, 17 - 24

McDonald, R.W. & St. Clair, C.C. (2004) The effects of artificial and natural barriers on the movement of small mammals in Banff National Park, Canada. *Oikos,* **105**, 397-407

Mills, M.G.L. & Gorman, M.L. (1997) Factors Affecting the Density and Distribution of Wild Dogs in the Kruger National Park. *Conservation Biology,* **11**, 1397-1406

Morales, J.M., Moorcroft, P.R., Matthiopoulus, J., Frair, J.L., Kie, J.G., Powell, R.A., Merrill, E.H. & Haydon, D.T. (2010) Building the bridge between animal movements and population dynamics. *Philosophical Transactions of the Royal Society B*, 365, 2289-2301

Osofsky, S.A., McNutt, J.W. & Hirsch, J.K. (1996) Immobilization and monitoring of free-ranging Wild Dogs (*Lycaon pictus*) using a Ketamine/Xylazine/Atropine combination, Yohimbine reversal and pulse oximetry. *Journal of Zoological Wildlife Medicine,* **27**, 528 - 532

Shepard, D.B., Kuhns, A.R., Dreslik, M.J. & Phillips, C.A. (2008) Roads as barriers to animal movement in fragmented landscapes. *Animal Conservation,* **11**, 288-296

Slotow, R.O.B. 2012. Fencing for Purpose: A case study of elephants in South Africa. *Fencing for Conservation: restriction of evolutionary potential or a riposte to threatening processes?*, (eds M. Somers & M.W. Hayward), pp. 91-104. Springer, New York

St. Clair, C.C. (2003) Comparative Permeability of Roads, Rivers, and Meadows to Songbirds in Banff National Park. *Conservation Biology,* **17**, 1151-1160

Stander, P.E. (1990) A Suggested Management Strategy for Stock-Raiding Lions in Namibia. *South African Journal of Wildlife Research,* **20**, 37-43

Tracey, J.A., Zhu, J., Boydston, E., Lyren, L. Fisher, R.N. & Crooks, K.R. (in press). Mapping behavioral landscapes for animal movement: A finite mixture modelling approach. *Ecology*, in press

Trombulak, S.C. & Frissell, C.A. (2000) Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities. *Conservation Biology,* **14**, 18-30

van der Meer, E., Moyo, M., Rasmussen, G.S.A. & Fritz, H. (2011) An empirical and experimental test of risk and costs of kleptoparasitism for African wild dogs (Lycaon pictus) inside and outside a protected area. *Behavioral Ecology and Sociobiology,* **22**, 985-992

Vanak, A.T., Thaker, M. & Slotow, R.O.B. (2010) Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation,* **143**, 2631-2637

Vercauteren, K.C., Lavelle, M.J. & Hygnstrom, S. (2006) Fences and Deer-Damage Management: A Review of Designs and Efficacy. *Wildlife Society Bulletin,* **34**, 191-200

Wiens, J.A., Crawford, C.S. & Gosz, J.R. (1985) Boundary Dynamics: A Conceptual Framework for Studying Landscape Ecosystems. *Oikos,* **45**, 421-427

Willems, E.P. & Hill, R.A. (2009) Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology,* **90**, 546 – 555

Zeller, K.A., McGarigal, K. & Whiteley A.R. (2012). Estimating landscape resistance to movement: a review. *Landscape Ecology*, 27, 777-797

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, USA.

FIGURES LEGENDS AND FIGURE

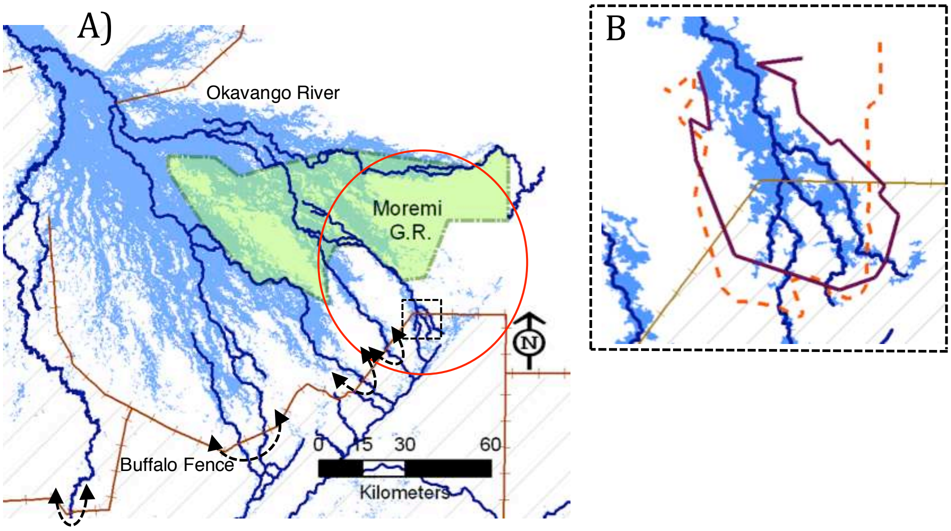

Fig. 1: The study area in the Okavango Delta, Northern Botswana and a qualitative representation of habitat connectivity for the species that easily cross the fence but not the rivers. The red circle (Panel A) highlights the two barrier types under investigation: a 60 km section of the Southern Buffalo Fence (brown, ticked line) and three effluents of the Okavango River, namely the Santantadibe, the Gomoti and the Khwai Rivers (from bottom to top and from left to right). Rivers and perennial floodplains are depicted in dark blue and light blue, respectively. Moremi Game Reserve is shown in green. During periods of high water levels, when rivers cross the fence, connectivity between the eastern and western side of the Delta, as well as between peninsulas may be almost only granted by individuals moving around the drying terminus of the rivers (black, dotted lines in Panel A, and enlarged section in Panel B) through, hostile, cattle farming areas (diagonal hatching). During periods of droughts, however, connectivity may be granted north of the fence by movements through dry sections of the rivers (see main text for more details). An enlarged section of the study area (Panel B) showing a 7 days and 53.5 km route of a group of wild dogs (solid purple line) and an 11 days and 54.2 km route of a cheetah (dashed orange line) that travelled around the drying terminus of the Gomoti River.

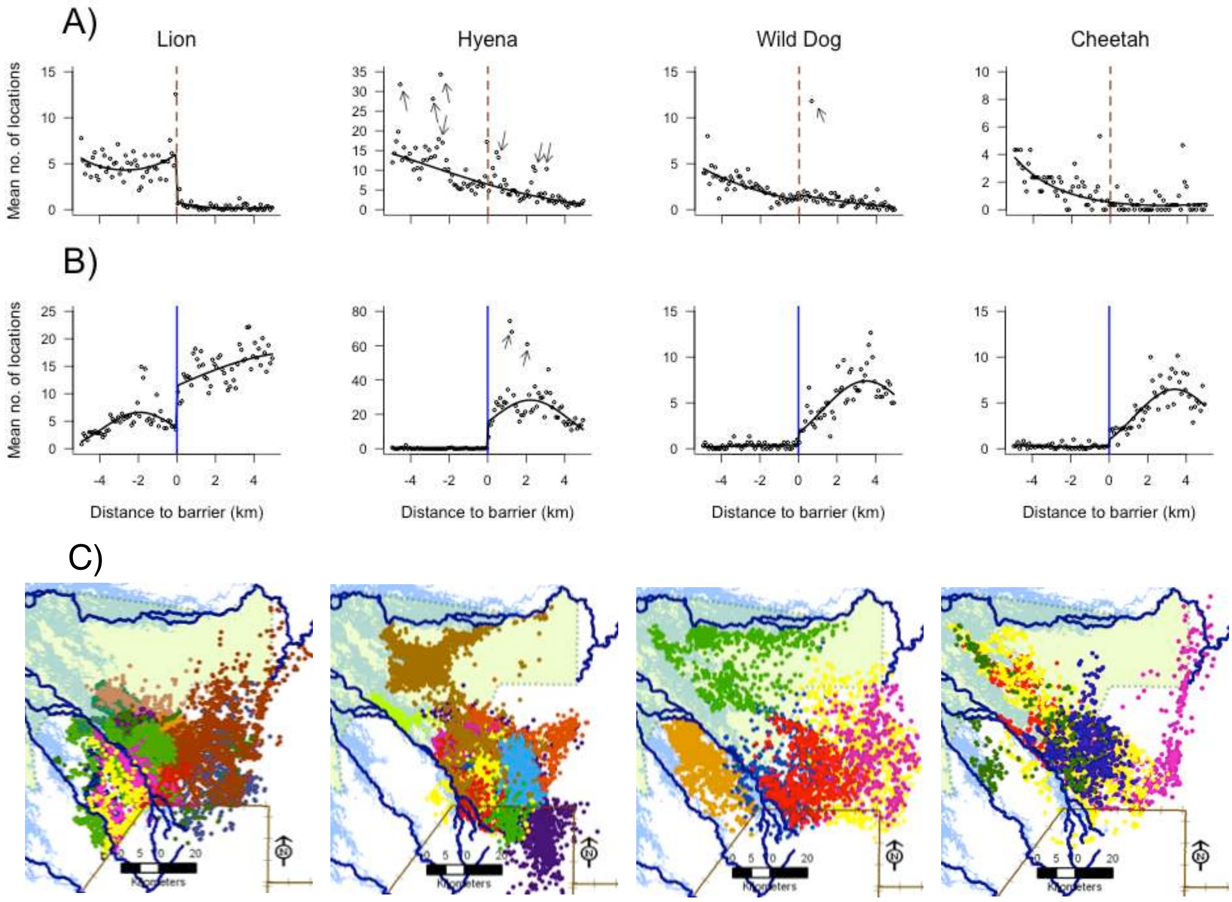

Fig. 2: Mean number of GPS locations (open dots) on either side of A) the fence (Panel A) the rivers (Panel B) and a spatial representation of the real distribution of each individual of the four species (Panel C). The black solid lines represent model fitted values; the line through the middle of the graphs represent the barriers; the arrows represent an increased number of locations due to the presence of large carcasses and den sites (Panels A & B). These outliers were not retained in the analyses unless otherwise specified. The geographic centre of all animals' territories was on the northern side of the fence (left of the middle line in Panel A) and on the eastern side of the river (right of the middle line in Panel B). Numbers of GPS locations were binned within 100-m width bands up to a maximal distance of 5 km from the barrier. See Fig. S1-S4 in the Supporting Information for an enlarged representation of the data distribution of each individual of the four species (Panel C).

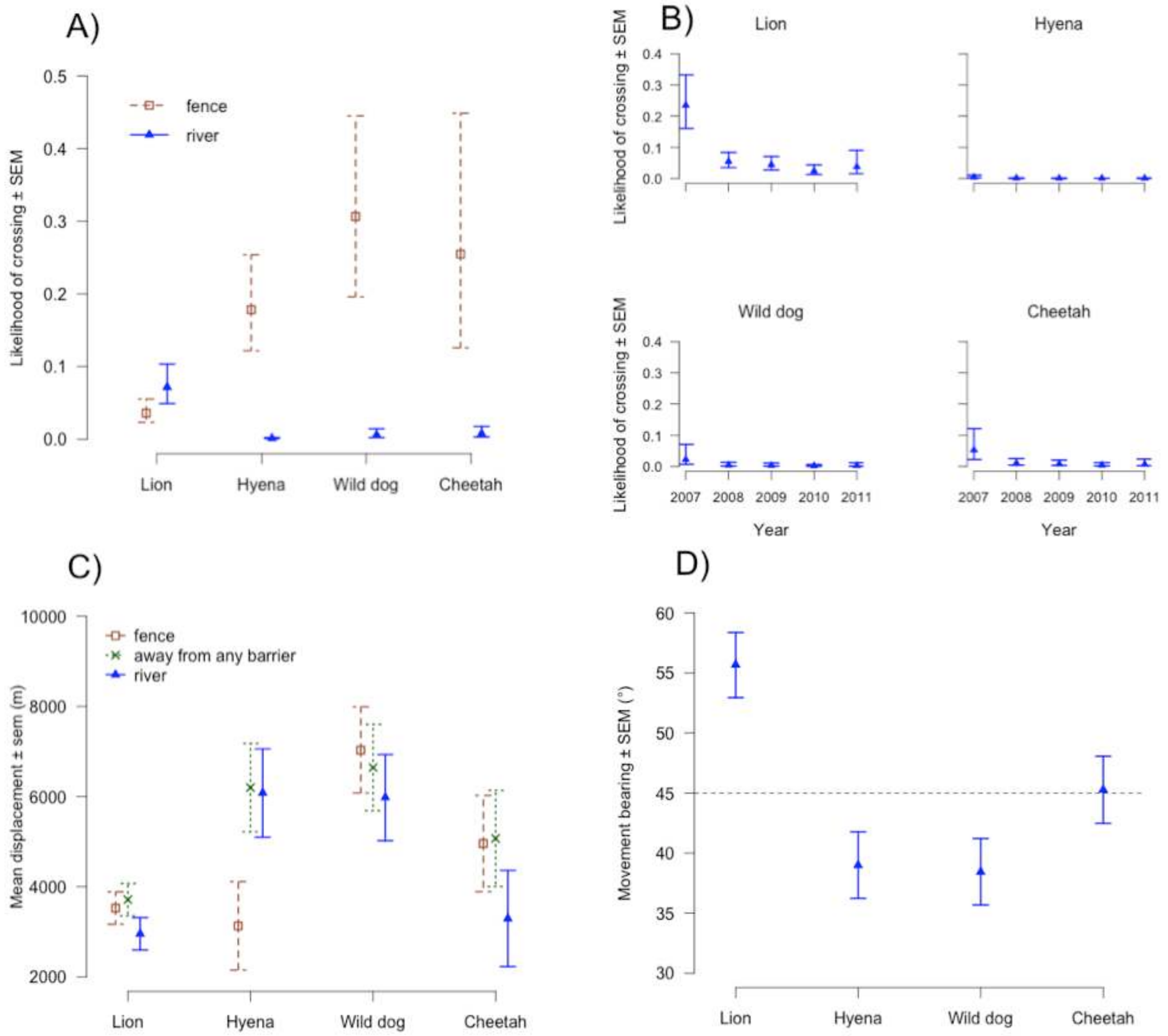

Fig. 3: Barrier crossing likelihood and movement metrics for four large carnivore species. Crossing likelihood was investigated by logistic regression for two different barrier types, the fence and the rivers (Panel A), and between years for the rivers (Panel B). Water levels in the rivers constantly increased between 2007 and 2011 due to exceptionally high precipitation. Net displacement between four consecutive 'steps' in the vicinity of the barriers and at random locations away from the barriers (Panel C) and movement bearings in the vicinity of the fence for the four species (Panel D). Values larger than 45° (dashed line) indicate the tendency of movements parallel to the fence, whereas values smaller than 45° indicate the tendency of perpendiculars movements to the fence.